

MORPHOLOGY AND RELATIONSHIPS
OF
ILLICIUM, SCHISANDRA AND KADSURA

I. STEM AND LEAF

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With six plates

INTRODUCTION

IN A PREVIOUS PAPER (1), we called attention to the fact that plants of general ranalian affinities may be divided upon the basis of their pollen morphology into two major categories, viz. (1) those resembling many monocotyledons in having monocolpate pollen or pollen phylogenetically derived from such types of microspores and (2) those resembling most dicotyledons in having tricolpate or derived types of pollen. All plants of the former category, with the exception of the aquatic Cabomboideae and Nymphaeoidae, have secretory cells of a fundamentally similar type. Such "resin" or "ethereal oil" cells do not occur in the second category of ranalian plants, except in *Illicium*, and the Schisandraceae. The secretory idioblasts of *Tetracentron* are of a different morphological type, being elongated and not infrequently ramified.

Since *Illicium*, *Schisandra* and *Kadsura* exhibit evidences of relationship to both major categories of ranalian plants and may prove to be significant in future discussions of the phylogeny of the dicotyledons, it is desirable that the three genera be re-examined from a broad morphological point of view. Material recently assembled by our colleague, Dr. A. C. Smith, for taxonomic revisions of *Illicium* and the Schisandraceae, has provided accurately identified specimens for such investigations. We have examined 34 of the 42 species of *Illicium*, 22 of the 25 species of *Schisandra*, and all of the 22 species of *Kadsura* recognized by Dr. Smith (9).

STEM: XYLEM

The young stem of *Illicium* is characterized by its unilacunar nodes, each leaf having at its base an arc-shaped strand of vascular tissues that is related to a single broad parenchymatous lacuna in the vascular cylinder of the vegetative axis, *Fig. 1*. The later-formed primary vascular elements of the internodal parts of the stem — in contrast to those of the Degeneriaceae, Himantandraceae, Magnoliaceae, Winteraceae, *Trochodendron*, *Tetracentron*, and *Euptelea* — are not aggregated in discrete bundles that are separated by conspicuous parenchymatous, interfascicular parts. The primary xylem tends to be more or less loosely and uniformly dis-

tributed in a pseudo-siphonostelic rather than in a typically eustelic-appearing arrangement.

The rays of the first-formed secondary xylem are uniseriate, vertically extensive and composed of "upright" cells, *Fig. 9*. Subsequently, certain of the ray initials of the cambium divide anticlinally, leading in later-formed wood, *Fig. 10*, to the transformation of parts of the original uniseriate rays into low, biseriate, triseriate or occasionally quadriseriate rays in which the long axis of the constituent cells is radially instead of vertically oriented, compare *Figs. 7* and *10*. Thus, the wood of older stems, in contrast to that of ordinary herbarium specimens, is characterized by having a typically "heterogeneous" type of ray structure. As demonstrated by Kribs (8) and Barghoorn (2), a commonly occurring trend of structural specialization in dicotyledons involves reduction or elimination of multiserial rays. In *Illicium*, this trend of specialization has progressed to a level where multiserial rays are eliminated from the first-formed secondary xylem and are reduced in width and height in the later-formed wood. The distribution of the wood parenchyma is transitional between diffuse and scanty abaxial paratracheal, *Fig. 7*.

Although the rays and the wood parenchyma of *Illicium* exhibit conspicuous evidences of phylogenetic modification, the tracheary elements are of relatively primitive types. The long, slender, thin-walled, angular vessel members have extensively overlapping ends with numerous bars in their scalariform perforation plates. The pitting between vessels, and between vessels and parenchyma, is scalariform with transitions to opposite-multiseriate. The imperforate tracheary elements have conspicuous bordered pits and are essentially thick-walled tracheids from a morphological point of view. The vessels are diffusely distributed throughout the secondary xylem, pore multiples being of infrequent or sporadic occurrence. Where growth layers are clearly differentiated in the secondary xylem, the vessels of the earlywood may be somewhat larger than are those of the latewood, *Fig. 7*.

The young stems of *Schisandra* and *Kadsura* have unilacunar nodes, but differ from those of *Illicium* in forming tripartite foliar traces, *Fig. 4*. The internodal parts of the stems exhibit a wide range of variability both in the arrangement of the primary xylem and in the detailed structure of the secondary wood. In certain of them, *Fig. 14*, the primary xylem occurs in relatively widely spaced strands, i.e., in a typically eustelic arrangement; whereas in others, *Fig. 13*, the vessels of the last-formed primary xylem appear as a continuous ring, i.e., in transverse sections of the internode.

The secondary xylem may be dense and of a relatively primitive structural type, *Fig. 14*, or it may be of a highly specialized and extremely porous type such as occurs commonly in many scandent plants, *Fig. 8*. The first-formed secondary xylem frequently is of the former type, transition to increasing porosity occurring during subsequent stages of the enlargement of the stem, *Fig. 14*. In other cases, the cambium first forms a narrow zone of nearly vesselless xylem which is succeeded by an abrupt

and precocious transition to a conspicuously porous type of wood, *Fig. 13*. Certain stems exhibit more or less clearly defined zones of alternating density and porosity.

As indicated in *Fig. 14*, the inner zones of unmodified secondary xylem are characterized by having slender diffusely scattered vessels, thick-walled tracheids, multiseriate rays that extend outward from the interfascicular parts of the eustele and numerous intervening high-celled uniseriate rays. The distribution of wood parenchyma is scanty diffuse and abaxial paratracheal. Such secondary xylem — allowing for differences due to its ontogenetic position — resembles the wood from older stems of *Illicium*, compare *Figs. 7* and *14*, but a majority of its vessels differ from those of *Illicium* in having a reduced number of bars and enlarged openings in their scalariform “perforation plates.” Vessel members exhibiting early stages of their phylogenetic derivation from scalariformly pitted tracheids are, however, of not infrequent occurrence. In contrast to this relatively primitive type of secondary xylem, the highly specialized porous type of wood illustrated in *Fig. 8* is characterized by its huge vessels, its large, thin-walled, profusely pitted tracheids, and its more abundantly developed paratracheal parenchyma. In structurally more specialized stems, the rays of the first-formed secondary xylem are prevailingly uniseriate, *Fig. 13*, certain of them subsequently broadening to multiseriate rays. The larger vessels have perforation plates with a single large circular or oval opening. The pits between such vessels and parenchyma are conspicuously enlarged, having large apertures and more or less vestigial borders on the vessel side. Where vessels are in contact, the pitting is scalariform or transitional to opposite. Alternating seriations of bordered pits occur at times between vessels and tracheids.

It is evident, accordingly, that the xylem of *Illicium* is of a relatively uniform and stable type. On the contrary, the wood of *Schisandra* and *Kadsura* exhibits a wide range of structural variability, as is so commonly the case in scandent plants. Conspicuous structural differences occur not only in stems of different species, but also in different stems from presumably the same species and even in different shoots of the same plant. A wealth of specially collected material must be examined before it will be possible to determine the exact significance of anatomical criteria in differentiating species and varieties. Such intensive investigations of the scandent schisandras and kadsuras should prove, however, to be extremely significant from both morphological and physiological points of view.

STEM: PHLOEM

In addition to rays, the recently formed phloem of *Illicium* consists of numerous contiguous sieve tubes among which are scattered companion cells, phloem parenchyma strands and cambiform cells of a special type. The long, slender sieve tube members have extensively overlapping ends with numerous, often widely separated, sieve areas. The cells of the rays and of the parenchyma strands have large vacuoles that contain a high

ratio of tannin or other phenolic compounds. The cambiform cells have layered "mucilaginous" contents which expand rapidly in water and stain intensely with ruthenium red. As a stem increases in diameter, sclereids tend to be formed sooner or later in the older, outer secondary phloem. These more or less ramified stone cells may be diffusely scattered or they may be aggregated in compact masses of varied form. Slender, thick-walled fibres are confined to the primary body and when present in the stem are diffusely scattered about the outer periphery of the stele in the so-called pericyclic zone.

The phloem of *Schisandra* and *Kadsura* resembles that of *Illicium* in containing numerous elongated or cambiform elements with stratified "mucilaginous" contents. The "mucilage cells" of the first-formed phloem commonly tend to become more or less extensively dilated, *Fig. 12*, in contrast to those of the subsequently formed secondary phloem which retain a more slender form, as in the phloem of *Illicium*.

There is a more precocious development of sclerenchyma in the secondary phloem of *Schisandra* and *Kadsura* than in homologous tissue of *Illicium*, and the more or less extensively clustered, thick-walled, lignified elements are of an entirely different morphological type. In contrast to the ramified stone cells of *Illicium*, the sclerenchymatous elements of *Schisandra* and *Kadsura* are of a linearly elongated and fiberlike form, *Fig. 26*. As noted by Solereder (10), the thick, lamellated, unpitted secondary wall of these cells develops asymmetrically, gradually crowding the protoplast laterally toward the periphery of the cell, *Fig. 23*. During the last stages of secondary wall formation, numerous crystals of calcium oxalate become encysted in the outer surface of the cellulose adjacent to the constricted protoplast. This asymmetry in the development of the secondary wall and in the distribution of crystals occurs characteristically in the sclerenchymatous elements of all species of *Kadsura* and *Schisandra*. As will be shown on subsequent pages, diversified forms of this crystal-bearing sclerenchyma occur more or less abundantly in the cortex and pith of the stem, in the leaf and the flower, and thus are a significant diagnostic characteristic of the Schisandraceae.

"Pericyclic" fibers are more abundantly developed in the Schisandraceae than in *Illicium*. They differ markedly from the crystal-bearing sclerenchymatous elements of the secondary xylem, having normal symmetrically developed walls, and being conspicuously pitted and septate. They commonly appear as a more or less continuous zone or ring in cross sections of young stems. However, this ring of "pericyclic" fibers becomes disrupted into disconnected arcs or strands during subsequent enlargement of the stem. Not infrequently the earlier breaks in the "pericyclic" ring become occluded by crystal-bearing sclerenchymatous elements of bizarre forms.

STEM: CORTEX AND PITH

Three types of idioblasts are of more or less frequent occurrence in the cortex and pith of *Illicium*. Globular "resin" or "ethereal oil" cells,

having a tenuous "suberized" inner membrane which stains in sudan IV, occur commonly in the cortex. They vary considerably in size and number. "Mucilage" cells of diversified size and form and of fluctuating abundance may be formed in both the cortex and the pith. More or less conspicuously branched sclereids occur at times in the cortex or in both the cortex and the pith.

The cortex and the central part of the pith are badly collapsed in most herbarium specimens of *Schisandra* and *Kadsura*, and, therefore, are poorly preserved for anatomical investigations. It is evident, however, that globular "ethereal oil" cells are of common occurrence in the cortex, *Fig. 12*, and that "mucilage" cells frequently are present in the succulent central core of the pith. Furthermore, crystal-bearing sclerenchymatous elements are formed in the cortex and not infrequently in the pith. These cells fluctuate widely in size, form, and number in different stems. They may be abundantly developed throughout the cortex and pith of the internodal parts of the stem or they may be few in number and confined to the nodal parts.

LEAF: EPIDERMIS AND STOMATA

Throughout the genus *Illicium* the lateral walls of the lower epidermis, as seen in surface view of the leaf, are conspicuously pitted and undulating, *Fig. 11*. It should be noted in this connection, however, that drying and reagents which tend to contract the epidermis may accentuate the undulations, whereas treatments that excessively reexpand the cells and cell walls reduce or eliminate the wavy outlines. The lateral walls of the upper epidermis may be either smooth or undulating.

The cuticle of the under surface of the leaf is commonly characterized by having parallel, ridge-like thickenings. These projections of the outer surface of the cuticle, *Fig. 11*, may be coarse and conspicuous or very fine and easily obscured in preparing leaves for microscopic examination. They are distributed in specific patterns, e.g., oriented parallel to the long axis of the mid-rib and the larger veins, concentrically about the stomata and radially in the rosettes of cells surrounding the secretory cells of the lower epidermis, *Fig. 11*. They may be uniformly distributed, or confined to restricted areas, viz. about the stomata, the secretory cells, or the larger veins. Ridge-like thickenings of the cuticle may occur also on the upper surface of the leaf.

According to Solereder (10), the stomatal guard cells of *Illicium Griffithii* (?) and *I. religiosum* (?) have lobe-like appendages that are oriented along extensions of the major axis of the aperture. Similar structural appearances occur in nearly all of the 73 collections of *Illicium* examined by us and, therefore, are characteristic of the genus. When the lower epidermis is examined unstained in surface view, the stomata exhibit a deceptive, superficial resemblance to those of Gramineae, see Haberlandt (7), where the guard cells are shaped like dumb-bells, having dilated thin-walled ends connected by a slender very thick-walled part. The lobe-like

appearances are also suggestive of the lightly cutinized polar areas in Bennettitalean stomata, see Florin (5).

That the stomatal apparatus of *Illicium* is actually of a fundamentally different type may be demonstrated, however, by examining strips of the epidermis and thin transverse sections of the leaf that have been stained with sudan IV.¹ In such preparations, the hypothetical lobe-like appendages prove to be tapered, intercellular intrusions of the cuticle between the constricted ends of the guard cells, compare *Figs. 16* and *17*. When the stomatal apparatus is examined in surface view at upper focal levels, these intrusions are seen to be in continuity with broad arcs of cutin which project inward between the guard cells and adjacent epidermal cells, the combined cuticular intrusions resembling a head with a broad-brimmed hat, *Fig. 17*. These intercellular intrusions of the cuticle fluctuate considerably in form as seen in surface and sectional views, but tend to be massive except in *I. floridanum* Ellis and certain collections of *I. parviflorum* Michaux, where they are reduced to tenuous wedges of cutin. In surface view, the outlines of the paired guard cells vary from narrowly to broadly elliptical, the dimension of the major axis fluctuating from 30 to 70 microns with corresponding variations in the minor axis. Each pair of guard cells is accompanied by 2 to 4 subsidiary cells oriented parallel to them, *Fig. 17*. These subsidiary cells appear to have been derived from the same mother cell as the guard cells. Subsidiary cells that are adjacent to guard cells tend to broaden internally and to underlie the guard cells, *Figs. 15* and *17*. Occasionally the internal expansion is so extensive that the subtending parts of the subsidiary cells become concrescent, thus sealing the stoma internally. Where two subsidiary cells are formed lateral to a guard cell, *Fig. 17*, the one adjacent to the guard cell frequently has a narrow exposed outer surface. In certain cases, so little of the cell is exposed that it is easily overlooked in surface view except under high magnification.

Most leaves of *Illicium* have comparatively thick cuticles within which a conspicuous vestibule or entrance to each stoma is formed, *Fig. 15*. The size and form of this cuticular vestibule fluctuate widely, not only in different collections of *Illicium*, but also in different parts of the same leaf. The outer aperture of the vestibule may be large or small, narrowly or broadly elliptical, or more or less rectangular in surface view, due in part to variations in the form and the extension of the outer rim-like projection

¹ Strips of cuticle with attached epidermal cells were obtained by macerating pieces of leaf in a mixture of equal volumes of 5% chromic and 5% nitric acids at a temperature of 56° C. These were then washed, stained in sudan IV and mounted in glycerine. If the macerating treatment is unduly prolonged, the cuticle is modified and loses its staining capacity in sudan IV.

Sections of leaves were prepared by soaking pieces of the lamina in hot water, then in either warm (45° C.) lactic acid or glycerine for two days. The pieces of leaves were then washed, dehydrated, embedded in paraffin, serially sectioned, bleached in concentrated hydrogen peroxide, stained in Haidenhain's haematoxylin and sudan IV and mounted in glycerine.

of the cuticle, *Fig. 15*. There is also more or less extensive internal cutinization subtending the guard cells. The rim-like projections of these cutinized parts commonly are in contact in closed stomata, whereas the walls of the guard cells are not.

In contrast to the tough, leathery, entire leaves of *Illicium*, those of *Schisandra* and *Kadsura* are softer, thinner and commonly provided with more or less numerous serrations. The lateral walls of the epidermal cells may be conspicuously pitted and undulating, but these characters are less pronounced and constant than they are in most species of *Illicium*. Although the cuticle is in general much thinner, it frequently exhibits a more or less conspicuous ribbing which closely resembles that which occurs so conspicuously in *Illicium*. There is a similar radial pattern in the rosettes of cells that surround the secretory cells of the lower epidermis. Furthermore, there are at times similar, but less massive, intrusions of cutin between the ends of the guard cells, *Figs. 18* and *19*. In such cases, there usually are no intrusions of cutin between the ends of the guard cells and adjacent epidermal cells, such as occur so characteristically in the stomatal apparatus of *Illicium*, *Fig. 17*.

The stomata are relatively large, the outline of the paired guard cells fluctuating between narrowly and broadly elliptical and having as in *Illicium* a major axis of from 30 to 70 microns. The subsidiary cells of the stomatal apparatus fluctuate widely in size, form, number and arrangement even within the limits of a single leaf. At one extreme are stomata that have subsidiary cells oriented parallel to the guard cells, as in *Illicium*, *Fig. 17*. At the other extreme of structural variability are guard cells that are subtended by parts of ordinary epidermal cells of diversified form. Numerous transitions between these structural extremes are of common occurrence, *Figs. 18* and *19*. Whether all or certain of the subsidiary cells are derived from the same primordial cell as the guard cells can be determined only by detailed ontogenetic and cytological investigations.

LEAF: VASCULARIZATION

The leaves of *Illicium* are characterized by having a simple, arc-shaped strand of vascular tissues that extends throughout the petiole and the mid-rib of the lamina, *Figs. 1-3*. On the contrary, the leaves of *Schisandra* and *Kadsura* usually have three discrete strands of vascular tissues in the petiole, *Fig. 5*, and the basal part of the lamina. The three separate bundles are replaced, however, by a single arc with involute margins in the central and apical parts of the lamina, *Fig. 6*. Occasionally aberrations occur in this typical pattern of vascularization. In certain cases, the three strands of primary vascular tissue may be bridged by cambial activity. Conversely, division may occur at times, giving rise to more than three strands in the petiole.

LEAF: IDIOBLASTS

Three types of idioblasts, viz. "resin" cells, "mucilage" cells and ramified sclereids, may be present in the leaf, as in the stem, of *Illicium*.

No sclereids are present in the lamina of 30 of the 73 collections of this genus examined by us. In 22 cases, they are diffusely distributed throughout the mesophyll, whereas in 21 of the collections they are confined to tissue in close proximity to the mid-rib. Sclereids occurring in the more spongy parts of the mesophyll tend to be profusely ramified and of highly diversified forms. The lumen may be relatively large and the branches conspicuously tapered, *Fig. 20*, or the lumen may be vestigial and the branches nearly cylindrical with blunt apices, *Fig. 21*. Sclereids in close proximity to the mid-vein and the vascular tissue of the petiole frequently tend to be massive, to have rectangular outlines in sectional views, and to be provided with contorted branches or with broad irregular lobes, *Fig. 22*. The foliar sclereids of *Illicium* differ from those of *Trochodendron*, see Foster (6), in their smaller size, their less extensive branching and in having smooth, rather than spiculate, outer surfaces.

It should be noted in these connections that the mid-vein and the larger lateral veins usually have a coating of slender, thick-walled fibres, comparable to the "pericyclic" fibres of the stem. Such fibres do not occur, however, about the terminal veinlets which are entirely devoid of sclerenchymatous elements, except in one collection of *I. majus* Hook.f. and Thomson, *Lau 28772*. "Pericyclic" fibres may be present or absent in the petiole.

The foliar "ethereal oil" or "resin" cells of *Illicium* fluctuate considerably in size and abundance. They tend to occur in the spongy mesophyll and the lower epidermis, and to be infrequent, if not invariably absent, in palisade tissue and the upper epidermis. Although they usually are spherical or ovoid in form, they may at times become somewhat lobate in tissue having large intercellular lacunae. Those that originate in the lower epidermis expand inwardly among the subepidermal cells of the leaf. As previously stated, their exposed outer part forms the center of a characteristic rosette of radially oriented epidermal cells, *Fig. 11*.

The size, form and distribution of "mucilage" cells should be studied in freshly collected leaves from living plants, dried leaves from herbarium specimens being unfavorable material for this purpose. In many cases, these cells appear to be confined to the palisade tissue, as observed by Blenk (3) in three species of *Illicium*.

The foliar "ethereal oil" cells of *Schisandra* and *Kadsura* resemble those of *Illicium* in general size, form and distribution, those of the lower epidermis forming the center of similar rosettes of radially oriented epidermal cells. The vascular strands of the petiole and the veins of the lamina differ, however, from those of *Illicium* in having conspicuous and more or less extensively dilated "mucilage" cells of elongated form in the primary phloem (darkly stained cells in *Figs. 5* and *6*). The leaves of *Schisandra* and *Kadsura* also differ markedly from those of *Illicium* in the character and the distribution of sclerenchymatous elements. Typical pitted, symmetrically thickened and profusely ramified, sclereids do not occur in the former genus. As in the case of the stem, the sclerenchymatous elements

of the leaf are of an unpitted, asymmetrically thickened and crystal-bearing type. They fluctuate widely in size, form and distribution, *Figs.* 24-29.

In the sections *Pleiostema*, *Maximowiczia* and *Euschisandra* of *Schisandra* and in the section *Cosbaea* and part of the section *Sarcocarpon* of *Kadsura*² crystal-bearing sclerenchyma is absent in the lamina and is confined to the basal part of the petiole. In these plants, such cells are usually absent in the pith of the internodal parts of the stems. On the contrary, in the section *Sphaerostema* of *Schisandra* and in the section *Eukadsura* and part of the section *Sarcocarpon* of *Kadsura*, crystal-bearing sclerenchyma occurs, not only in the petiole, but also in the lamina of the leaf. In most cases, the more or less elongated crystal-bearing elements are scattered along the vascular bundles, veins and veinlets, with their long axis oriented parallel to that of the vascular elements. There are, however, several species in the section *Sarcocarpon* of *Kadsura* which exhibit conspicuous aberrations. In *K. marmorata* (E. G. and A. Henderson) A. C. Sm., *Elmer* 11718, *K. lanceolata* King, *M. R. Henderson* 11562, *K. borneensis* A. C. Sm., *J. and M. S. Clemens* 31889, and *K. Clemensiae* A. C. Sm., *J. and M. S. Clemens* 22115 (type), the crystal-bearing elements either are oriented at right angles to the veins or their elongated ends protrude freely into the mesophyll. In *K. marmorata*, some of these sclerenchymatous cells occur independently in the mesophyll and are not related in development to the veins.

The form and the distribution of ordinary pitted fibers are less stereotyped in leaves of *Schisandra* and *Kadsura* than they are in the foliar organs of *Illicium*. The veins and the terminal veinlets may be heavily jacketed by such elements or they may be devoid of them. Not infrequently short fibrous elements are scattered along the veins much as are the elongated crystal-bearing cells. Particularly in the section *Sarcocarpon* of *Kadsura*, there are transitions from elongated fibrous elements to short, broad, irregularly shaped, pitted cells that jacket the terminal veinlets.

DISCUSSION

Illicium obviously is a genus that exhibits a number of relatively stable structural characters in its vegetative organs. Particularly significant in this connection are the uniformity of its unilacunar nodal anatomy, the characteristic vascularization pattern of its leaf, the pseudo-siphonostelic rather than typically eustelic-appearing arrangement of its primary vascular tissues, the specific combinations of primitive and specialized anatomical features of its secondary xylem and phloem, and the curious intercellular intrusions of the cuticle in its stomatal apparatus.

In contrast to *Illicium*, *Schisandra* and *Kadsura* exhibit a combination of relatively stable and highly variable anatomical characters. On the one hand, there is considerable uniformity in the nodal anatomy, the vascularization pattern of the leaf, the presence of conspicuously dilated

² For lists of the species included in these sections see Smith (9).

“mucilage” cells in the primary phloem, and the occurrence of curious, asymmetrically thickened, crystal-bearing elements, particularly in the secondary phloem. On the other hand, there is a wide range of variability in the structure of the stomata and especially in the vascular tissues of the stem. The xylem fluctuates — even within the limits of a single plant — from a relatively primitive type to extremes of structural specialization.

What conclusions may be deduced from such anatomical data regarding the affinities of the three genera? How should the various anatomical criteria be weighed in so doing? What actually are the merits of including these genera within the Magnoliaceae? Significant answers to these questions must be based upon a broad knowledge of the behavior of anatomical characters in a wide range of dicotyledonous families. Due allowances must be made for commonly occurring structural similarities due to parallel or convergent evolution, and for differences due to excessively divergent trends of morphological specialization in plants of certain habits of growth, e.g., vines.

During the last 30 years, extensive investigations of the vascular tissues in all of the principal orders and families of the dicotyledons have revealed and clarified the salient trends of phylogenetic specialization that occur in these tissues. Thus, it now is possible in many cases to assess the evolutionary significance of specific combinations of structural characters in the vascular tissues. Unfortunately, there is as yet no comparable body of reliable information regarding the epidermis, cortex and pith of the stem and the epidermis and mesophyll of the leaf in dicotyledons. Therefore, there is no conclusive evidence available at present for determining whether the ancestral dicotyledons actually possessed certain specific types of stomata, secretory cells, sclerenchyma, etc.

The vegetative organs of *Schisandra* and *Kadsura* are so similar and exhibit such similar ranges of structural variability that the two genera can be separated at present only upon the basis of differences in their reproductive parts. The Schisandraceae differ, however, from other woody plants of ranalian affinities in the occurrence within them of a peculiar and distinctive type of crystal-bearing sclerenchyma and in peculiarities of structural specialization in the xylem of the stem. How significant are such anatomical differences? Do they preclude relatively close genetic relationship, for example between *Illicium* and the Schisandraceae? It should be emphasized in this connection that differences of comparable magnitude occur not infrequently in families having both arboreal and scandent representatives. In fact, the structural differences in the xylem are no greater than those that differentiate arboreal from scandent species of such genera as *Bauhinia* and *Gnetum*. Therefore, in comparing *Illicium* and the Schisandraceae, it is essential to allow for the acceleration of structural specialization in plants, viz. *Schisandra* and *Kadsura*, that have acquired a climbing habit of growth.

Fortunately, the first-formed secondary xylem of vines and lianas frequently affords valuable clues regarding the general level of structural

specialization in the trees or shrubs from which such scandent plants were derived. Thus, the inner wood in the less modified parts of the stems of *Schisandra* and *Kadsura* clearly indicates that these genera were derived from plants having a typically eustelic structure and a relatively primitive type of secondary xylem in which the multiseriate rays extended outward from the interfascicular parts of the eustele. Although the first-formed secondary xylem in the less modified parts of *Schisandra* and *Kadsura* resembles the later-formed wood of *Illicium*, it is evident that these scandent genera cannot have been derived directly from *Illicium*. This is due to the fact that modification of the eustele and reduction of the multiseriate rays is more advanced in *Illicium* than in the scandent genera.

However, the available anatomical evidence does not negate the derivation of the three genera from a common ancestor. Such a possibility of relatively close genetic relationship between *Illicium* and the Schisandraceae is strengthened by similarities in the cuticles, the stomata, the "ethereal oil" cells and particularly the "mucilage" cells of these plants. "Ethereal oil" cells and stomata, having subsidiary cells oriented parallel to the guard cells, are of common occurrence in various families of the more woody ranalian complex, and taken by themselves are not indicative necessarily of specific, rather than of generalized, ranalian affinities. On the contrary, the peculiar elongated or cambiform "mucilage" cells, which occur so characteristically in the phloem of *Illicium* and the Schisandraceae, have not been encountered by us in other woody representatives of the ranalian complex. Furthermore, the unilacunar nodes of *Illicium*, *Schisandra* and *Kadsura* — in contrast to the prevailingly trilacunar or multilacunar nodes of the Winteraceae, Degeneriaceae, Himantandraceae, Magnoliaceae, Trochodendraceae, etc. — are likewise indicative of possibly close genetic relationship.

Detailed studies of the comparative anatomy of the vegetative organs of woody ranalian families reveal no cogent evidence for including either *Illicium* or the Schisandraceae in the Magnoliaceae. When constituted of the ten genera — *Liriodendron*, *Magnolia*, *Manglietia*, *Michelia*, *Talauma*, *Kmeria*, *Aromadendron*, *Alcimandra*, *Pachylarnax* and *Elmerrillia* — as suggested by Dandy (4), the Magnoliaceae are a very natural grouping of plants which exhibit a relatively high degree of structural uniformity in all of their vegetative and reproductive parts. The inclusion of *Drimys* and its allies, *Illicium*, *Schisandra*, and *Kadsura* introduces structurally incongruous elements which are only remotely related to the Magnoliaceae (*sensu stricto*). Thus, the wide evolutionary gap between the vesselless xylem of the Winteraceae and that of the vessel-bearing Magnoliaceae precludes close relationship between the two groups of plants, as does the unusually high degree of structural specialization and complexity in the nodes and leaves of the Magnoliaceae. Similarly, widely divergent and entirely different trends of structural specialization in the xylem, phloem, nodes and leaves of *Illicium*, *Schisandra*, and *Kadsura* serve as a serious obstacle to the inclusion of these genera in the Magnoliaceae. That such

conclusions are strengthened by detailed investigations of the reproductive parts of these plants will be shown in a subsequent paper. The significance of recent publications of Lemesle and Ozenda will be discussed in this second contribution.

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EXPLANATION OF PLATES

PLATE I

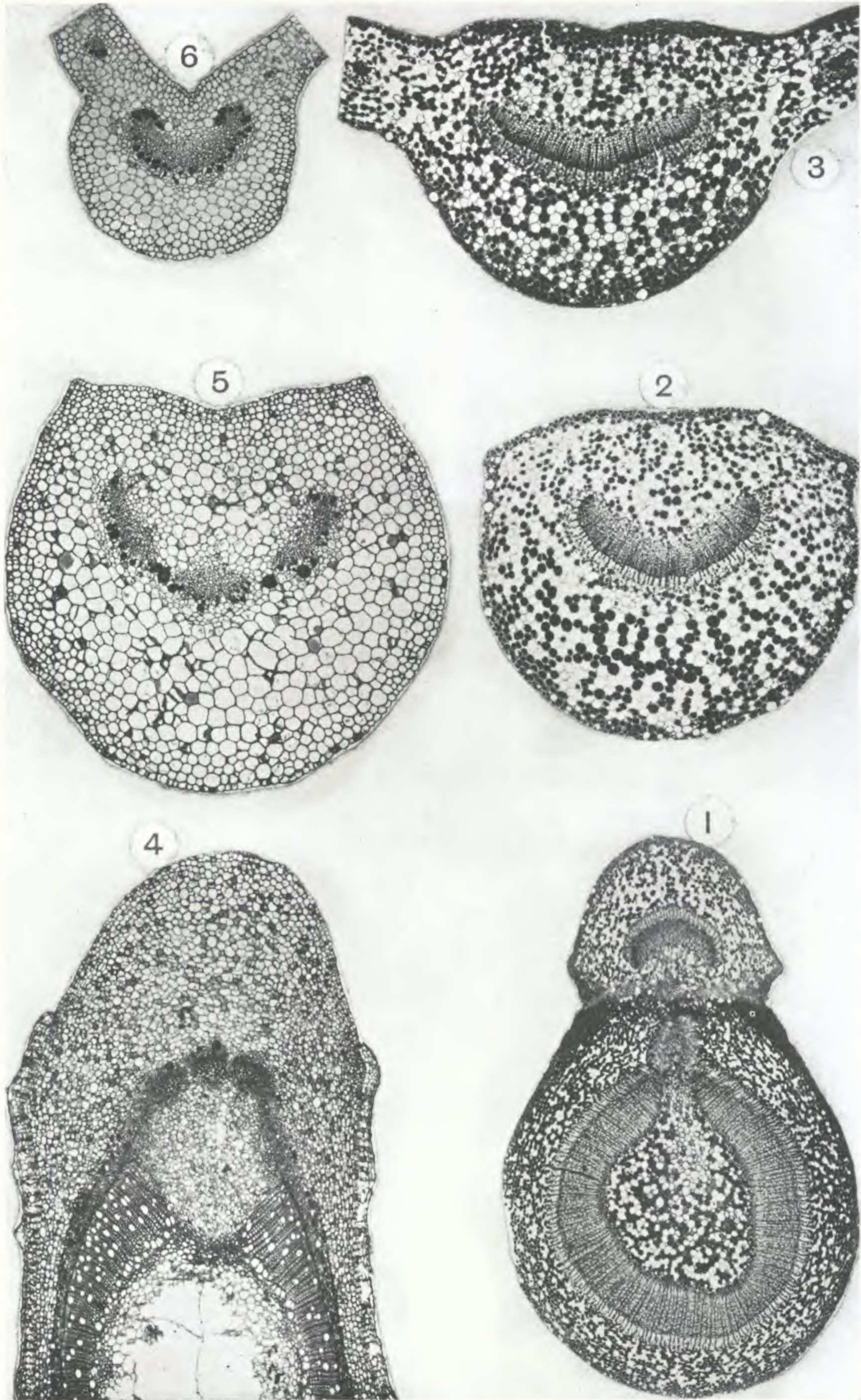
FIG. 1. *Illicium anisatum* L. *H. U.* 15749. Transverse section of the unilacunar node. $\times 10$. FIG. 2. *I. anisatum*. *H. U.* 17326. Transverse section of the petiole showing single broad arc of vascular tissues. $\times 18$. FIG. 3. *I. anisatum*. *H. U.* 17326. Transverse section of the leaf, showing broad arc of vascular tissues. $\times 18$. FIG. 4. *Schisandra chinense* (Turcz.) Baill. *H. U.* 17371. Transverse section of the unilacunar node, showing three separate vascular strands at the base of the leaf. $\times 13$. FIG. 5. *S. chinense*. *H. U.* 17370. Transverse section of the petiole showing three separate strands of vascular tissues. $\times 18$. FIG. 6. *S. chinense*. *H. U.* 17370. Transverse section of the leaf showing single arc of vascular tissues. $\times 18$.

PLATE II

FIG. 7. *Illicium*. *Y. U.* 24057. Transverse section of the wood from the outer part of an old stem, showing heterogeneous rays and distribution of vessels and wood parenchyma. $\times 120$. FIG. 8. *Kadsura scandens* (Bl.) Bl. *H. U.* 17341. Transverse section of the wood, showing huge vessels, large thin-walled tracheids and abaxial paratracheal wood parenchyma. $\times 120$.

PLATE III

FIG. 9. *Illicium*. *H. U.* 15763. Tangential longitudinal section of wood close to the primary body showing uniseriate rays only. $\times 120$. FIG. 10. *Illicium*. *H. U.* 11175. Tangential longitudinal section of wood from the outer part of an older stem, showing both uniseriate and triseriate rays. $\times 120$. FIG. 11. *I. Masa-Ogatai* (Makino) A. C. Smith. *Kanehira* 3386. Lower surface of the leaf showing stomata, secretory cell, ribbed cuticle and undulating contour of epidermal cells. $\times 250$.



MORPHOLOGY OF ILLICIUM, SCHISANDRA AND KADSURA